

New target-strength model indicates more krill in the Southern Ocean

David A. Demer and Stéphane G. Conti

Demer, A. D., and Conti, S. G. 2005. New target-strength model indicates more krill in the Southern Ocean. — ICES Journal of Marine Science, 62: 25–32.

Antarctic krill, *Euphausia superba*, comprises the foundation of the foodweb in the Southern Ocean and is the target of a large fishery. Recently, the total abundance of krill in the Scotia Sea was estimated from an international echosounder and net survey (CCAMLR 2000) to be 44.3 million metric tonnes (Mt; CV 11.4%) (Hewitt *et al.*, 2002). The new biomass estimate prompted the Antarctic Treaty's Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) to revise the precautionary catch level for krill in the area from 1.5 to 4 Mt (SC-CAMLR, 2000). These survey results are based on the total echo energy attributed to krill, scaled by the Greene *et al.* (1991) model of krill acoustical reflectivity or target strength (TS). Presented here is a re-analysis of the CCAMLR 2000 data incorporating recent improvements in the characterization of krill TS. The results indicate that the estimated krill biomass in the Scotia Sea may be as high as 192.4 Mt (CV = 11.7%), or as low as 109.4 Mt (CV = 10.4%), depending solely on the expected distribution of krill orientations. The new Stochastic, Distorted-Wave, Born-Approximation (SDWBA) TS model solved with an empirically estimated distribution of *in situ* orientations leads to a krill-biomass estimate that is nearly 2.5 times the previous estimate. In consequence, revisions may be warranted of the standard krill TS model, the CCAMLR 2000 biomass estimate, and the associated precautionary catch level for krill in the Scotia Sea.

© 2004 Published by Elsevier Ltd on behalf of International Council for the Exploration of the Sea.

Keywords: Abundance, CCAMLR 2000, *Euphausia superba*, krill orientations, SDWBA model, target strength.

Received 26 March 2004; accepted 12 July 2004.

D. A. Demer and S. G. Conti: Advanced Survey-Technologies Program, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA, 92037, USA. Correspondence to D. A. Demer: tel: +1 858 546 5603; fax: +1 858 546 5608; e-mail: david.demer@noaa.gov

Introduction

Antarctic krill, *Euphausia superba*, comprises the foundation of the foodweb in the Southern Ocean and is the target of a large fishery (Hewitt and Linen Low, 2000). Recently, the total abundance of krill in the Scotia Sea was estimated from an international echosounder and net survey (CCAMLR 2000) to be 44.3 million metric tons (Mt; CV 11.4%) (Hewitt *et al.*, 2002). The new biomass estimate prompted the Antarctic Treaty's Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) to revise the precautionary catch level for krill in the area from 1.5 to 4 Mt (SC-CAMLR, 2000).

The accuracy of the acoustic krill-biomass estimate depends on many components of the survey design and analysis such as the surveyed area, the species-identification algorithm, and the animal mass-versus-length model, but is largely dictated by the accuracy of the TS model

(Demer, *in press*). In a model developed by Greene *et al.* (1991), TS is linearly related to the logarithm of the standard krill length (L ; nearest mm distance from the anterior tip of the eyes to the posterior end of the uropods, excluding their terminal setae). It was derived from measurements of a variety of crustaceans but not Antarctic krill, at an acoustic frequency (f) of 420 kHz (Wiebe *et al.*, 1990). The *de facto* international standard frequency for surveying Antarctic krill is 120 kHz. The ratio of acoustic wave numbers ($k = 2\pi f/c$) is used to transform the model to different f at a selected sound speed (c) (Greene *et al.*, 1991):

$$TS_f = 34.85 \log_{10} L - 127.45 + 10 \log_{10} (k_f/k_{120 \text{ kHz}}). \quad (1)$$

Using TS measurements of live Antarctic krill including caged aggregations (Foote *et al.*, 1990), *in situ* individuals (Hewitt and Demer, 1991), and captive individuals (Pauly

and Penrose, 1998), the model was corroborated at 120 kHz for a small range of L (Hewitt and Demer, 1991; SC-CAMLR, 1991). Subsequently, CCAMLR provisionally adopted a 120 kHz version of the Greene *et al.* (1991) model as an international standard for estimating krill biomass (SC-CAMLR, 1991).

Retrospectively, however, these TS data from caged and captive individuals suggested to Pauly and Penrose (1998) that the Greene *et al.* model may overestimate krill TS. Hewitt and Demer (1991) also recognized that their *in situ* data could be positively biased due to scattering from multiple targets being misinterpreted as that from individuals; and a comprehensive study by Demer *et al.* (1999) strongly supported their earlier suspicion.

Motivated by TS measurements that were inconsistent with the Greene *et al.* model's predictions, others (Demer and Martin, 1995) emphasized changes in TS due to variations in animal shape, morphology, and orientation, for which the model does not take account. Moreover, the Greene *et al.* model was not intended for use in the Rayleigh-scattering regime (Greene *et al.*, 1991), because it is fundamentally inaccurate when the acoustic wavelength is much larger than the animal size (Demer, in press). To improve upon the recognized limitations of the Greene *et al.* model, a physics-based model (DWBA) was proposed (McGehee *et al.*, 1998) that predicts krill TS as a function of f , incidence angle of the acoustical wave (ϕ), and animal length, shape, and material properties. The DWBA is based upon the coherent summation of scattering from cylindrical elements of a discretized bent cylinder (idealized krill shape). McGehee *et al.* proposed a generic krill shape (McGehee *et al.*, 1998) based upon dimensions of krill that had been fasting for over six months. They noted, however, that Antarctic krill can have broadly varying shapes depending upon their feeding condition, gender, and maturity stage, and that krill sizes and target strengths should be measured from animals in their natural state. Nevertheless, the DWBA was empirically validated with TS measurements from the fasting krill at $f = 120$ kHz near broadside incidence, but large disparities (5–20 dB) were observed between measurement and theory at other angles, with predicted scattering less than measurements (McGehee *et al.*, 1998). Thus, the importance of knowing the *in situ* distribution of krill orientations was underscored.

Possibly the best quantitative information about *ex situ* orientations of Antarctic krill come from studies of krill swimming in elaborate aquaria (Kils, 1981; Endo, 1993). The normal distribution ($N[\bar{\theta}, \text{s.d.}]$) of krill orientations relative to horizontal ($\theta = 90^\circ - \phi$) measured by Kils' ($\theta = N[\bar{\theta} = 45.3^\circ, \text{s.d.} = 30.4^\circ]$) was quite similar to that measured independently by Endo ($\theta = N[\bar{\theta} = 45.6^\circ, \text{s.d.} = 19.6^\circ]$), but the latter distribution was narrower.

Qualitative *in situ* observations have been made by scuba divers (Hamner *et al.*, 1983), and more recently via underwater video with a sample image shown in Figure 1.

Hamner *et al.* (1983) observed that all individuals in a school assumed virtually the same orientation and usually swam horizontally at $\theta \leq 10^\circ$. In contrast, the video of swarming krill suggests that the krill assumed all orientations with equal probability (i.e. a uniform distribution). Perhaps, neither of these *in situ* observations are relevant to the behaviour of krill beneath a survey vessel moving at 10 knots.

Kils observed that krill swim backwards at $\theta > 55^\circ$, hover at $50^\circ \leq \theta \leq 55^\circ$, and swim forwards at $\theta < 50^\circ$, with lower angles corresponding to faster swimming speeds (Kils, 1981). Moreover, Endo (1993) found that krill may also change their orientations depending upon their maturity stage. Comparing daytime and night-time observations of krill, Everson (1982) observed an 8.5 dB reduction in mean volume scattering which could be due to diel changes in krill-orientation distributions. It is therefore probable that their orientation distribution depends on their activity and condition (e.g. hovering while feeding; migrating up, down, or horizontally; swimming against a current to maintain a preferred position; or fleeing from a predator, diver, or survey vessel).

For the measurements in aquaria, the animals may not have behaved naturally because of their being confined and the lack of current. In the cases of *in situ* observations of krill swarms, the presence of divers and the video camera lights may have affected their behaviour. While a recent study indicates that a survey vessel did not affect the behaviour of krill (Brierley *et al.*, 2002), this possibility should still be considered, especially for krill residing near the sea surface. Therefore, in the context of acoustical surveys of krill abundance, it is important to know the orientation distribution of krill beneath a survey vessel. Unfortunately, there is no published information in this regard.

Solving the DWBA with Kils' orientation distribution (Kils, 1981), expected values of krill TS were shown

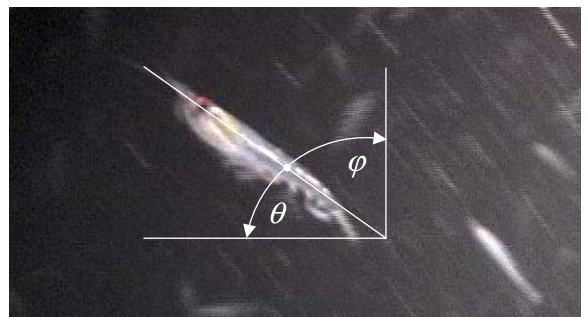


Figure 1. *Euphausia superba* in a swarm observed *in situ* off Cape Shirreff, Livingston Island, Antarctica on 6 February 2000. A digital video camera was lowered into a krill swarm at about 70-m depth and the orientation angles of the krill were qualitatively observed. The krill did not exhibit coordinated movements and assumed all orientation angles. The camera lights may have altered the krill's natural behaviour. In this case, $\theta = 44.6^\circ$ or $\phi = 45.4^\circ$.

(McGehee *et al.*, 1998) to be 6–8 dB lower than those predicted by the Greene *et al.* model and *in situ* TS measurements of krill (Hewitt and Demer, 1991). Use of these TS would increase current krill-biomass estimates by a factor of 4–6. Solving the DWBA with Endo's orientation distribution would result in an even larger negative disparity in TS and larger increases in biomass estimates. For TS predictions to approach *in situ* measurements, the DWBA must be solved with an improbably narrow distribution of krill orientations centred on normal incidence ($\theta = N[0^\circ, \sim 3^\circ]$), irrespective of the model's inaccuracies off the main scattering lobe.

The disparities between theory and measurements were explained (Demer and Conti, 2003a, b) using a new model (Stochastic DWBA or SDWBA) that accounts for the stochastic nature of sound scattering, noise, and flexure in the animal's body as it swims. The SDWBA model was corroborated (Demer and Conti, 2003b; Demer and Conti, 2004) using a new technique (De Rosny and Roux, 2001) that permits good measurement accuracy and precision (Demer *et al.*, 2003). Broad-bandwidth measurements were made of sound scattering from live Antarctic krill having a large range of sizes ($L \sim 20$ –50 mm). Solving the SDWBA model with a krill shape 40% fatter than the generic shape (McGehee *et al.*, 1998), based upon the relative dimensions of the measured krill to the generic krill shape (Demer and Conti, 2004), the rms difference between the model predictions and the scattering measurements was less than 0.2 dB over the frequencies from 60 to 202 kHz. The measurements at lower frequencies were slightly higher than theory and the discrepancies were attributed to noise.

Conversion of the broad-bandwidth measurements to an accurate prognosticator of krill TS requires knowledge of the *in situ* krill-orientation distribution beneath the survey vessel (Demer and Conti, 2003a). To measure *in situ* krill-orientation distributions that have spatio-temporal relevance to acoustic-survey analyses, multi-frequency and broad-bandwidth techniques have been proposed (Chu *et al.*, 1993; Martin-Traykovski *et al.*, 1998). In these techniques, acoustic backscatter spectra are used to infer krill orientations from inversions of an accurate scattering model.

Methods

Using the krill length distributions measured during the CCAMLR 2000 survey and Kils' and Endo's krill-orientation distributions, the SDWBA model was solved for the differences in volume-backscattering strengths (Sv) at 120 and 38 kHz. These probability density functions were then compared rather disappointingly to the Sv differences measured from RV "Yuzhmorgeologiya" during the CCAMLR 2000 survey (Figure 2). A much better match between theory and the measurements was

obtained using $\theta = N[15^\circ, 5^\circ]$, later referred to as the Demer and Conti distribution of krill orientations.

The SDWBA was then evaluated for a krill 40% fatter than the generic krill shape (McGehee *et al.*, 1998) using 100 realizations of random phase ($sd = 0.7071$ radian), averaged over the three orientation distributions (Demer and Conti, Kils, and Endo), and compared to the Greene *et al.* model (Figure 3).

For further validation of the new TS model, the SDWBA solutions were also plotted vs. kL and compared to the Greene *et al.* model and a variety of krill TS measurements (Figure 4). For each of the three orientation distributions, a simplified function was fit to the SDWBA curves (SDWBA_{Demer and Conti}, SDWBA_{Kils}, and SDWBA_{Endo}) in the least-squares sense:

$$TS(kL) = A \left[\frac{\log_{10}(BkL)}{BkL} \right]^C + D(kL)^6 + E(kL)^5 + F(kL)^4 + G(kL)^3 + H(kL)^2 + IkL + J + 20 \log_{10} \left(\frac{L}{L_0} \right), \quad (2)$$

with coefficients and reference length (L_0) in Table 1.

To verify the metric used in the initial CCAMLR 2000 data analysis for acoustically identifying *E. superba* (Hewitt *et al.*, 2002), Equation (2) was evaluated at 120 and 38 kHz vs. L , and the resulting functions were subtracted (Figure 5). Then, substituting Equation (2) for the standard TS model (Greene *et al.*, 1991; SC-CAMLR, 2000), new krill-biomass estimates and their associated coefficients of variation were calculated as in Hewitt *et al.* (2002), and tabulated for each of the three krill-orientation distributions and three survey frequencies (Table 2).

Results

The Demer and Conti distribution of krill orientations ($\theta = [15^\circ, 5^\circ]$) provides the best fit to the differences in Sv at 120 and 38 kHz measured during the CCAMLR 2000 survey (Figure 2). Judging from an empirical characterization of krill swimming speeds vs. their orientations (Kils, 1981), this distribution of orientations corresponds to krill swimming relatively horizontally and fast (on the order of 5–10 cm s⁻¹ or 2–3 body lengths per second).

The SDWBA model solved with the Demer and Conti distribution of orientations predicts TS's that are consistently lower than for the Greene *et al.* model, but higher than those computed with the Kils and Endo distributions (Figure 3). TS values lower than the Greene *et al.* model result in higher krill-biomass estimates.

For values of kL_0 from 0 to 50, the simplified SDWBA (Equation 2) has an rms error of 0.2 dB, and a maximum inaccuracy of 0.4 dB relative to the SDWBA (Figure 4). The differences between the TS predicted by the simplified SDWBA at 120 and 38 kHz vs. krill length provide a metric for acoustically identifying *E. superba* (Figure 5). These

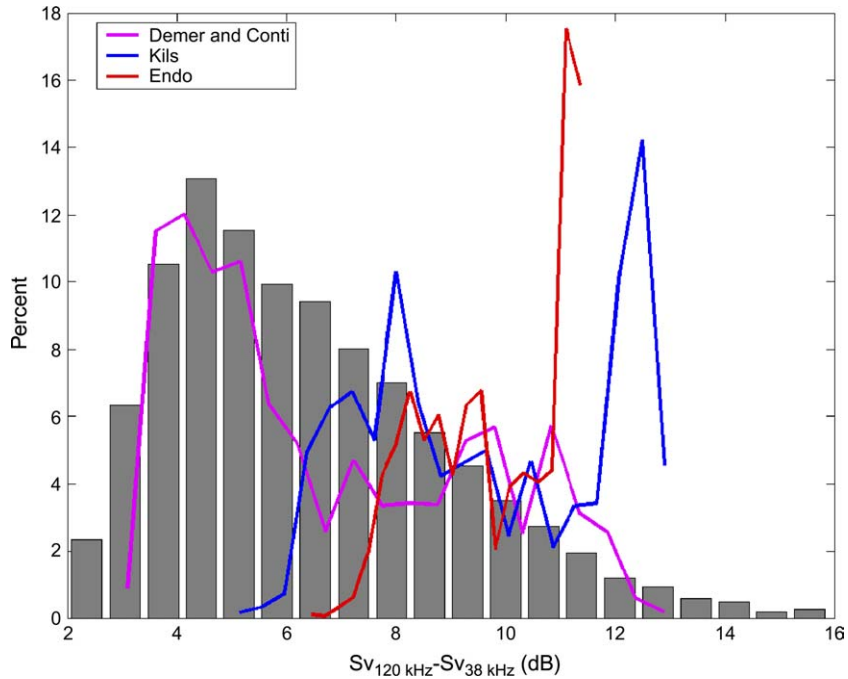


Figure 2. The differences in volume-backscattering strengths (Sv) attributed to krill at 120 and 38 kHz measured from RV “Yuzhmorgeologiya” during the CCAMLR 2000 survey (grey bars), compared to predictions from the SDWBA model solved with the CCAMLR 2000 krill-length frequency distribution and three krill-orientation distributions: Demer and Conti (magenta), Kils (blue), and Endo (red). The Demer and Conti distribution of krill orientations ($\theta = N[15^\circ, 5^\circ]$) provided the best fit to the empirical data.

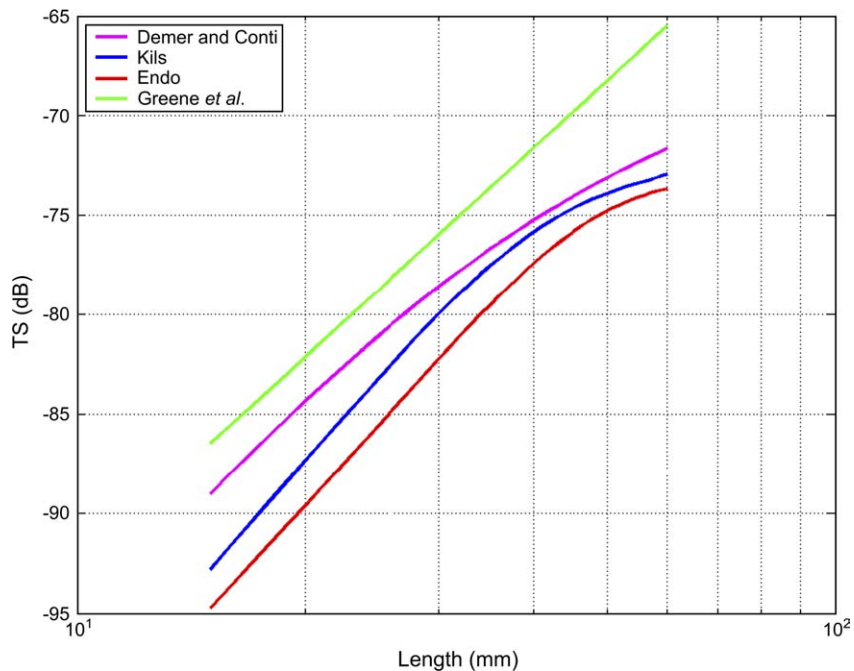


Figure 3. Krill TS at 120 kHz as predicted by the SDWBA model averaged over three distributions of animal orientations (Demer and Conti, $\theta = N[15^\circ, 5^\circ]$), magenta; Kils (1981), $\theta = N[45.3^\circ, 30.4^\circ]$, blue; and Endo (1993), $\theta = N[45.6^\circ, 19.6^\circ]$, red), and the Greene *et al.* model (green). Comparing the Greene *et al.* model with the SDWBA solved with the Demer and Conti orientation distribution, the differences between the TS predicted by the two models range from about 3 to 7 dB depending on the krill lengths.

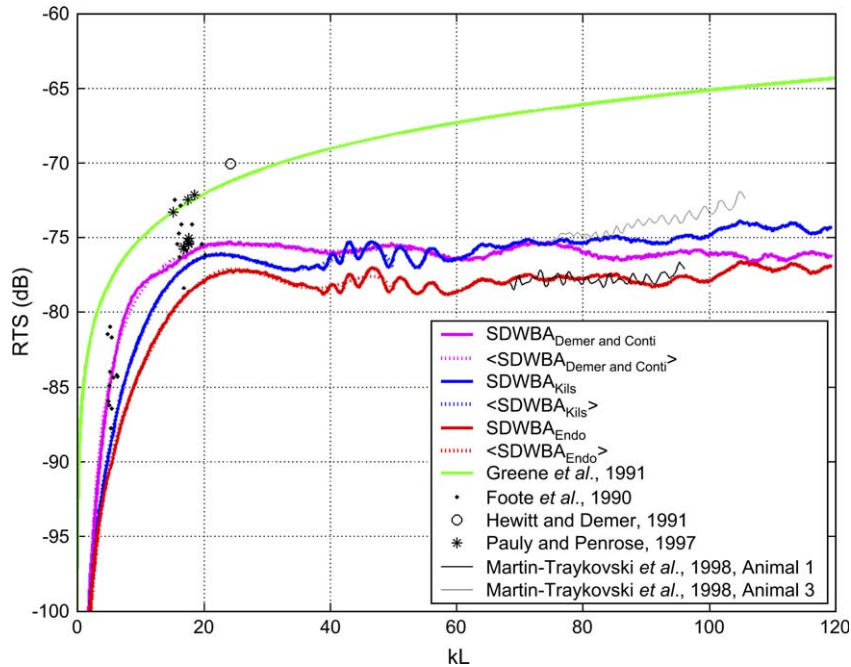


Figure 4. Reduced target strengths [$RTS = TS - 20 \log(L/L_0)$] predicted by the SDWBA averaged over three distributions of animal orientation (Demer and Conti, $\theta = N[15^\circ, 5^\circ]$; Kils (1981), $\theta = N[45.3^\circ, 30.4^\circ]$; and Endo (1993), $\theta = N[45.6^\circ, 19.6^\circ]$), and simplified versions of the same ($\langle SDWBA \rangle$; see Equation 2), and the Greene *et al.* model [$RTS_f = 34.85 \log_{10}(L_0) - 127.45 + 10 \log_{10}(k_f/k_{120 \text{ kHz}})$]. Also plotted are krill TS data measured *in situ* with a split-beam, 120-kHz echosounder (Hewitt and Demer, 1991); inferred from volume backscatter at 38 and 120 kHz from aggregations of krill (Foote *et al.*, 1990); measured from many individual live krill in a tank at 120 kHz (Pauly and Penrose, 1998), and measured from two live animals over a broad-bandwidth (425–600 kHz) (Martin-Traykovski *et al.*, 1998) and averaged over the Demer and Conti orientation distribution. The *in situ* TS data may be biased high due to the likelihood of multiple targets being interpreted as individuals (Hewitt and Demer, 1991; Demer *et al.*, 1999). While most of these empirical data do not explicitly account for krill-orientation distributions, they appear to invalidate the Greene *et al.* model at low kL and match the SDWBA model best at high kL.

Table 1. Coefficients and reference length (L_0) for the simplified SDWBA model of krill TS (Equation 2), averaged over Demer and Conti's, Kils' (1981), and Endo's (1993) distributions of krill orientations. Exponential notation ($*10^x$) is denoted by "e+x".

Equation (2) coefficients

	Demer and Conti	Kils	Endo
A	-9.30429983e+2	-4.34331668e+2	-2.69247212e+2
B	3.21027896e+0	3.22204281e+0	3.75866618e+0
C	1.74003785e+0	1.31770787e+0	1.04235848e+0
D	1.36133896e-8	4.91530057e-10	-3.29670608e-8
E	-2.26958555e-6	-1.78147825e-6	3.88024848e-6
F	1.50291244e-4	2.30291987e-4	-1.28707135e-4
G	-4.86306872e-3	-1.07519865e-2	-3.00255041e-4
H	7.38748423e-2	2.09995538e-1	7.29805964e-2
I	-4.08004891e-1	-1.50697031e+0	-8.41482900e-1
J	-7.39078690e+1	-7.13352566e+1	-7.17517841e+1
L_0	3.835e-2 (m)	3.835e-002 (m)	3.835e-002 (m)

predictions are consistent with the method employed in the original analysis of the CCAMLR 2000 survey data. That is, *E. superba* are characterized by $Sv_{120 \text{ kHz}} - Sv_{38 \text{ kHz}}$ in the range of 2–16 dB (Hewitt *et al.*, 2002).

By replacing the Greene *et al.* model with the SDWBA TS model, the abundance of *E. superba* in the Scotia Sea is re-estimated here to be 109.4 Mt (CV = 10.4%), 137.4 Mt (CV = 10.8%), or 192.4 Mt (CV = 11.7%), depending solely on the expected distribution of krill orientations (Demer and Conti, Kils, and Endo, respectively).

Discussion

Use of the SDWBA TS model solved with the Demer and Conti distribution of orientations results in approximately equal biomass estimates at measurement frequencies of 38 and 120 kHz (107.1 Mt and 109.4 Mt, respectively), and the lowest coefficients of variations for biomass estimates at all frequencies. Estimated consumption rates of krill predators suggest that these estimates are realistic (Everson *et al.*, 1990).

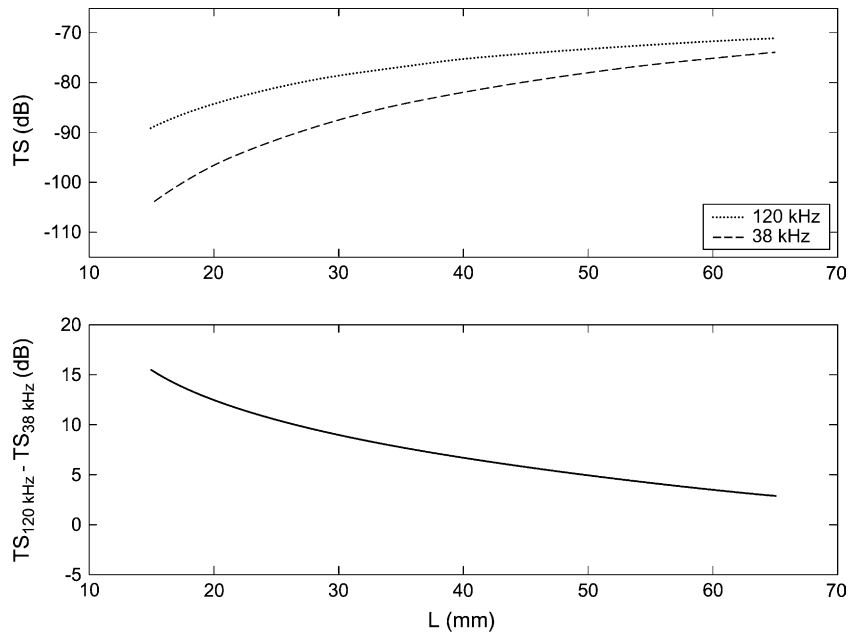


Figure 5. (a) The SDWBA TS model solved with the Demer and Conti distribution of krill orientations and two commonly used echosounder-survey frequencies (38 kHz, dashed line; and 120 kHz, dotted line); and (b) the differences in these predicted TS vs. standard krill length (L). The relative sound scatter at these two frequencies is used to acoustically identify krill (Hewitt *et al.*, 2002). The SDWBA model predictions are consistent with expectations that *E. superba* are characterized by differences in Sv at 120 and 38 kHz ranging from 2 to 16 dB (Hewitt *et al.*, 2002).

Use of the SDWBA TS model solved with the Demer and Conti distribution of orientations results in a krill-biomass estimate at 200 kHz that is 55% higher than those at the lower frequencies. This, however, could be due to zooplankton or other species being misinterpreted as krill

(Hewitt *et al.*, 2003) using the two-frequency technique for species identification (Hewitt *et al.*, 2002; Watkins and Brierley, 2003). Figures 2 and 5 indicate that all of sound scatter from *E. superba* matched the criteria, $2\text{ dB} \leq Sv_{120\text{ kHz}} - Sv_{38\text{ kHz}} \leq 16\text{ dB}$, and was therefore

Table 2. Conversion factors (C.F.) for converting integrated echo energy to krill biomass (Hewitt and Demer, 1993) resulting from the Greene *et al.* and SDWBA TS models, the associated krill-biomass estimates, and their coefficients of variation (CV). Using RMT8 net samples, three clusters of krill-length frequency distributions were identified for different portions of the CCAMLR 2000 survey area (Hewitt *et al.*, 2002). Cluster 1 is a narrow length distribution centred at 26 mm (small krill); Cluster 2 is a broad and somewhat bi-modal length distribution peaking at 46 mm (mixed sizes); and Cluster 3 is a positively-skewed length distribution centred at 52 mm (large krill). Here, the biomass estimate for the Greene *et al.* model at 120 kHz is 0.1 Mt less than that originally reported (i.e. 44.3 Mt; Hewitt *et al.*, 2002) owing to a reduction in rounding errors.

Orientation distribution	Frequency (kHz)	C.F. Cluster 1	C.F. Cluster 2	C.F. Cluster 3	Biomass (Mt)	CV (%)
Greene <i>et al.</i>	38	0.5163	0.4786	0.4661	31.8	9.3
	120	0.1636	0.1517	0.1477	44.2	11.4
	200	0.0981	0.0910	0.0886	44.8	15.7
Demer and Conti	38	2.7746	1.6174	1.4386	107.1	8.9
	120	0.2945	0.3907	0.4572	109.4	10.4
	200	0.2174	0.4092	0.5047	169.6	12.7
Kils	38	7.1187	4.0213	3.3641	264.3	9.0
	120	0.4403	0.4614	0.5537	137.4	10.8
	200	0.2559	0.5050	0.5372	200.0	12.9
Endo	38	9.4133	6.0572	5.3091	389.6	8.9
	120	0.7416	0.6237	0.6811	192.4	11.7
	200	0.3361	0.6982	0.8155	279.4	12.6

attributed to krill. However, it is likely that some sound scatter from other species was erroneously included, mostly in the 200-kHz measurements, resulting in a significant positive bias at that frequency (see Hewitt *et al.*, 2003). Relative to 38 and 120 kHz (wavelengths \approx 39.5 and 12.5 mm, respectively), sound scatter from animals smaller than *E. superba* is most appreciable at 200 kHz (wavelength \approx 7.5 mm).

The Demer and Conti distribution of orientations indicates that krill are most often oriented near horizontally and swimming quickly. This may characterize the average of multiple natural behaviours varying over the surveyed space and time, or an observation of krill's routine efforts to avoid the surveying vessel, or a combination of the two. If krill do avoid the survey vessel, or if echo energy from krill is otherwise excluded from the analysis, the acoustically estimated krill biomass can have an appreciable negative bias.

Besides the accuracy of the TS model, the estimated orientation distribution for krill beneath survey vessels, and possible avoidance behaviour, there are other potential components of measurement bias (Demer, *in press*). In particular, more research is needed on improved techniques for identifying and separating the echo energy from krill and coincident sound scatterers, the model of krill mass-versus-length, and the survey area presumed to include the stock. Such efforts to continually improve the method and to quantify the measurement uncertainty have made acoustical-survey data invaluable for fisheries research and management.

Conclusion

The CCAMLR 2000 survey results (Hewitt *et al.*, 2002) were based on the total echo energy attributed to krill, scaled by the Greene *et al.* (1991) model of krill TS. There is now a large body of evidence indicating that this krill TS model should be updated and a new standard adopted. The candidate SDWBA TS model (Demer and Conti, 2003a, b, 2004) solved with the Demer and Conti distribution of *in situ* orientations ($\theta = [15^\circ, 5^\circ]$) leads to a krill-biomass estimate of 109.4 Mt (CV = 10.4%), which is nearly 2.5 times the previous estimate of 44.3 Mt (CV = 11.4%). Therefore, revisions of the CCAMLR 2000 biomass estimate and the associated precautionary catch level for krill in the Scotia Sea may be warranted.

Acknowledgements

We are appreciative of the United States Antarctic Marine Living Resources Program for funding this study and most of the supporting investigations. Linda Martin-Traykovski (Woods Hole Oceanographic Institution) is thanked for graciously providing the broad bandwidth TS data in Figure 4. Roger Hewitt (US AMLR), Jon Watkins (British

Antarctic Survey), and Charles Greene (Cornell University) are thanked for their constructive criticisms of this work. Additionally, we thank Leif Knutsen, Big Foot Marine, for skilfully crafting a multi-instrumented small-boat, and Adam Jenkins, US AMLR, for expertly skipping RV "Ernest" in the coastal Southern Ocean, thereby facilitating the video observations sampled in Figure 1.

References

- Brierley, A. S., Fernandes, P. G., Brandon, M. A., Armstrong, F., Millard, N. W., McPhail, S. D., Stevenson, P., Pebody, M., Perrett, J. R., Squires, M., Bone, D. G., and Griffiths, G. 2002. An investigation of avoidance by Antarctic krill of RRS James Clark Ross using the Autosub-2 autonomous, underwater vehicle. *Fisheries Research*, 1448: 1–8.
- Chu, D., Foote, K. G., and Stanton, T. K. 1993. Further analysis of target-strength measurements of Antarctic krill at 38 and 120 kHz: comparison with deformed-cylinder model and inference of orientation distribution. *Journal of Acoustical Society of America*, 93(5): 2985–2988.
- Demer, D. A. An estimate of error for the CCAMLR 2000 estimate of krill biomass. Deep Sea Research, Part II, Special Issue on the CCAMLR 2000 Synoptic Survey (*in press*).
- Demer, D. A., and Conti, S. G. 2003a. Reconciling theoretical versus empirical target strengths of krill; effects of phase variability on the distorted-wave Born-approximation. *ICES Journal of Marine Science*, 60(2): 429–434.
- Demer, D. A., and Conti, S. G. 2003b. Validation of the stochastic, distorted wave Born-approximation model with broadbandwidth, total target-strength measurements of Antarctic krill. *ICES Journal of Marine Science*, 60: 625–635.
- Demer, D. A., and Conti, S. G. 2004. Erratum for: validation of the stochastic distorted-wave Born-approximation model with broadbandwidth, total target-strength measurements of Antarctic krill. *ICES Journal of Marine Science*, 61: 155–156.
- Demer, D. A., Conti, S. G., De Rosny, J., and Roux, P. 2003. Absolute measurements of total target strength from reverberation in a cavity. *Journal of Acoustical Society of America*, 113(3): 1387–1394.
- Demer, D. A., and Martin, L. V. 1995. Zooplankton target strength: volumetric or areal dependence? *Journal of Acoustical Society of America*, 98(2, Pt.1): 1111–1118.
- Demer, D. A., Soule, M. A., and Hewitt, R. P. 1999. A multiple-frequency method for potentially improving the accuracy and precision of *in situ* target-strength measurements. *Journal of Acoustical Society of America*, 105(4): 2359–2376.
- De Rosny, J., and Roux, P. 2001. Multiple scattering in a reflecting cavity: application to fish counting in a tank. *Journal of Acoustical Society of America*, 109: 2587–2597.
- Endo, Y. 1993. Orientation of Antarctic krill in an aquarium. *Nippon Suisan Gakkaishi*, 59(3): 465–468.
- Everson, I. 1982. Diurnal variations in mean volume-backscattering strength of an Antarctic krill (*Euphausia superba*) patch. *Journal of Plankton Research*, 4(1): 155–162.
- Everson, I., Watkins, J. L., Bone, D. G., and Foote, K. G. 1990. Implications of a new acoustic target strength for abundance estimates of Antarctic krill. *Nature*, 345(6273): 338–340.
- Foote, K. G., Everson, I., Watkins, J. L., and Bone, D. G. 1990. Target strengths of Antarctic krill (*Euphausia superba*) at 38 and 120 kHz. *Journal of Acoustical Society of America*, 87(1): 16–24.
- Greene, C. H., Stanton, T. K., Wiebe, P. H., and McClatchie, S. 1991. Acoustic estimates of Antarctic krill. *Nature*, 349: 110.

- Hamner, W. M., Hamner, P. P., Strand, S. W., and Gilmer, R. W. 1983. Behaviour of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling and molting. *Science*, 220: 433–435.
- Hewitt, R. P., and Demer, D. A. 1991. Krill Abundance. *Nature*, 353: 310.
- Hewitt, R. P., and Demer, D. A. 1993. Dispersion and abundance of Antarctic krill in the vicinity of Elephant Island in the 1992 austral summer. *Marine Ecology Progress Series*, 99: 29–39.
- Hewitt, R. P., Demer, D. A., and Emery, J. H. 2003. An eight-year cycle in krill-biomass density inferred from acoustic surveys conducted in the vicinity of the South Shetland Island during the austral summers of 1991/1992 through 2001/2002. *Aquatic Living Resources*, 16(3): 205–213.
- Hewitt, R. P., and Linen Low, E. H. 2000. The fishery on Antarctic krill: defining an ecosystem approach to management. *Reviews in Fisheries Science*, 8(3): 235–298.
- Hewitt, R. P., Watkins, J. L., Naganobu, M., Tshernyshkov, P., Brierley, A. S., Demer, D. A., Kasatkina, S., Takao, Y., Goss, C., Malyshko, A., Brandon, M. A., Kawaguchi, S., Siegel, V., Trathan, P. N., Emery, J. H., Everson, I., and Miller, D. G. M. 2002. Setting a precautionary catch limit for Antarctic krill. *Oceanography*, 15(3): 26–33.
- Kils, U. 1981. The swimming behaviour, swimming performance and energy balance of Antarctic krill *Euphausia superba*. *BIOMASS Scientific Series No. 3*. 122 pp.
- Martin-Traykovski, L. V., O'Driscoll, R. L., and McGehee, D. E. 1998. Effect of orientation on the broadband acoustic scattering of Antarctic Krill (*Euphausia superba*): implications for inverting zooplankton spectral-acoustic signatures for angle of orientation. *Journal of Acoustical Society of America*, 104(4): 2121–2135.
- McGehee, D. E., O'Driscoll, R. L., and Martin-Traykovski, L. V. 1998. Effects of orientation on acoustic scattering from Antarctic krill at 120 kHz. *Deep Sea Research II*, 45: 1273–1294.
- Pauly, T., and Penrose, J. D. 1998. Laboratory target-strength measurements of free-swimming Antarctic krill (*Euphausia superba*). *Journal of Acoustical Society of America*, 103(6): 3268–3280.
- SC-CAMLR, 1991. Report of the Tenth Meeting of the Scientific Committee (SC-CAMLR-X), CCAMLR, Hobart, Australia, 427pp.
- SC-CAMLR, 2000. Report of the Nineteenth Meeting of the Scientific Committee (SC-CAMLR-XIX), CCAMLR, Hobart, Australia.
- Watkins, J. L., and Brierley, A. S. 2003. Verification of acoustic techniques used to identify and size Antarctic krill. *ICES Journal of Marine Science*, 59: 1326–1336.
- Wiebe, P. H., Greene, C. H., Stanton, T. K., and Burczynski, J. 1990. Sound scattering by live zooplankton and micronekton: empirical studies with a dual-beam acoustical system. *Journal of Acoustical Society of America*, 88(5): 2346–2360.